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Some Points in the Anatomy of Chrysoma pauciflosculosa*

By Francis E. Lloyd

The material upon which these notes are based was collected by the writer on Cat Island, one of the Mississippi Sound series. This region lies in the northern edge of the tropical life zone, and is characterized by the presence of a goodly number of tropical strand plants.† *Chrysoma pauciflosculosa*, may be considered as one of these, indigenous to America, with a northern range extending to South Carolina on the Atlantic Coast. Its habitat according to Chapman ‡ is "sandy banks and shores," and appears to be a halophytic plant, at least in some localities. The plant is a shrub a meter or over in height, having vertical isolateral leaves. These are rigid, with three prominent longitudinal views, and are covered with an aromatic gummy exudate.

Using the floral characters as a basis the plant has been by some authors referred to the genus *Solidago*, from which it was separated first by Nuttall, who has been followed more recently by Greene. The reasons for which this has been done are found in the habit, woody character, and inflorescence of the plant. It is our present purpose to examine more particularly some points in the anatomy of the leaf.

In shape the leaf is narrowly elliptical, tapering into a short petiole. When examined by transmitted light it appears "pellucidly punctate" an appearance which is due to the peculiar arrangement of the internal tissues and not to accumulations of a secretion in cavities, as for example, in the Hypericaceae. Further observation by reflected light shows that each of the polygonal,

* Shortly before her death Dr. Emily L. Gregory, with whom two of her students, Miss Alice M. Isaacs and Miss Marion Satterlee, worked in collaboration, examined this plant. The results of their observations were presented in a paper read before the Torrey Botanical Club on January 14, 1896. Had Dr. Gregory's death not occurred, the paper would undoubtedly have been published. The writer has very kindly been given access to these results by Miss Isaacs, whom he wishes here to thank. The present paper is largely a verification of the observations presented in 1896.

† For a fuller account of this region see Lloyd, F. E., and Tracy, S. M., The Insular Flora of Mississippi and Louisiana Bull. Torr. Club, **28**: 61–101. 1901.

‡ Flora of Southern States.

pellucid areas is surrounded by a sulcus. In drying they shrink inwardly, giving rise to the term "pitted" as applied to the leaf surface, which however would better be described as a mosaic. Both sides of the leaf have the same appearance, the reason for which will be better understood by an examination of the internal structure.

The sulci just referred to are caused by the dipping down of the epidermis on both sides of the leaf to a depth equal approxi-

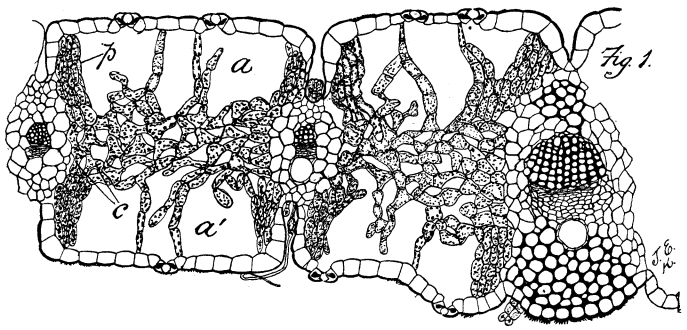

FIG. 1. Transverse section of leaf, through the midrib and two pairs of air chambers.

mately to one third of the thickness of the leaf. (Fig. 1.) The epidermal cells which line the sulcus are of gradually decreasing depth, the deeper they are placed. Between the sulci the epidermis stretehes almost without support. The arrangement of the mesophyll is such that there is thus formed a disposition of

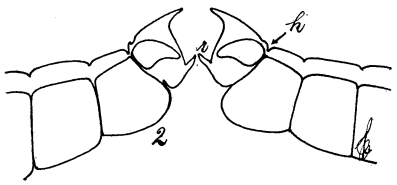

FIG. 2. Transverse section through a stoma.

tissues which suggests at once the well-known air chambers of the liverwort, *Marchantia*. In the roof of epidermal cells, which are cuticularized both within and without, are found the stomata, one of which is shown in detail in Fig. 2, in which are delineated the hinge line (*h*) and an inner guard ridge (*r*) making a sensitive and effective stoma. The effectiveness is heightened by the ac-

cessory cells lying adjacent, the presence of which in the Compositae is, so far as known, of rather rare occurrence, according to Benecke.* These cells are not, however, as well differentiated as in *Carlina* (Benecke, *l. c.*), but nevertheless serve to raise the stoma somewhat above the level of the epidermis, and, by the conformation of their walls, to aid in closing the aperture.

The stomata are to be found only in the "pellucid" areas, from the margins of which they are absent. In each area there are, on an average, about 22. They are found also upon the rounded edges of the leaf. The average size of the areas is 0.19 sq. mm. The stomata are therefore relatively numerous in the areas in which they occur.

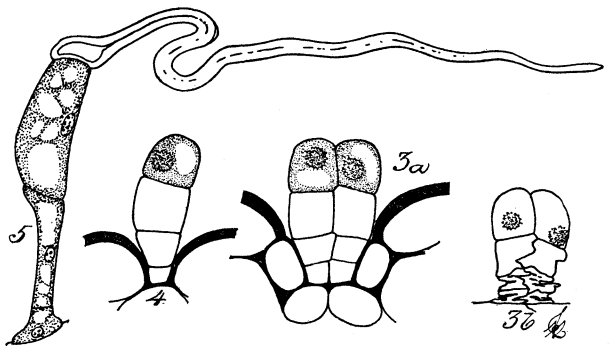

FIG. 3*a*, Double glandular hair; 3*b*, older condition, with collapsed cells; 4, single glandular hair; 5, whip hair.

The exposed surface of the leaf is entirely smooth and free from organs such as hairs. The cuticle is sculptured into irregular ridges, chiefly over the veins, and inconstantly over the rest of the surface. Two kinds of hairs grow in abundance at the bottoms of the sulci. Of these, one sort is glandular, the other, the so-called whip cells.†

The former are composed of two series of four cells each, the basal cells being the smallest (Fig. 3*a*). Their walls are thin and have a delicate cuticularized external layer. In the terminal cell one always finds a rounded mass of calcium oxalate crystals. In the mature leaf the three lower cells appear empty and are collapsed

* Bot. Zeit. 1892.

† Vesque, J., Caractères des * * * gamopetales * * * . Ann. Sci. Nat. Bot. VII., 1: 183. 1885.

while the terminal cell maintains its shape and contents. (Fig. 3*b*.) In type this form of hair agrees with that described by Vesque (*l. c.*) which he found at the base of the heads of *Chrysanthemum coronarium*. The contour differs however. Occasionally one finds such a hair composed of but one row of cells (Fig. 4). In all cases so far observed the two series of cells, when two are present, arise from two neighboring cells of the leaf, a fact which leads to the view that we have before us a case of concrescence. This must however be verified by a study of their development.

The whip hairs (Fig. 5), on the other hand, are quite different in form and function. They are composed of one series of four cells. The basal cell is lenticular, with or without a projecting portion. The second is a slender stalk-like cell; the third a thicker and somewhat longer cell, supporting at its outer end a long lash cell, four to five times as long as the rest of the hair. At the base of the lash cell is a bulbous enlargement upon which the lash is set obliquely, as occurs in similar hairs in *Carduus lanccolatus* (Vesque, *l. c.*). The lumen of the lash cell is almost obliterated except toward and at the base, and the thickened wall is composed of cellulose, with a very thin layer of cuticle which extends over the whole hair and is continuous with the cuticle of the leaf. The protoplasmic contents are plainly seen in all the cells of the hair except the lash cell, from which they appear to be absent in maturity. The whip cells, the lash of which is somewhat curled, usually protrude out of the sulcus and their slender ends lie upon the exposed leaf surface. They occur in greatest numbers at the juncture of the sulci.

When one asks concerning the function of these hairs the answer is more difficult for the whip cells than for the gland cells. From the latter is exuded the gummy secretion which renders the leaf more effectually protected against the loss of moisture. The activity of secretion is resident chiefly, or probably entirely, in the terminal cell, as is indicated by the accumulation of calcium oxalate. The whip cells occur, in cases so far as known, only as part of a tomentose or arachnoid covering (Vesque, *l. c.*). We may regard them here as useless morphological members, or we may ascribe to them some function, such as leading by capillarity the gummy secretion out upon the leaf surface exposed to the air. That this takes place there is no doubt, though that this is more than an incidental phenomenon may be doubted.

The mesophyll offers some points of very great interest. No palisade tissue may be said to exist in the ordinary acceptance of the term. Dorsiventral differentiation is quite absent. We do find, however, a distinct division into two forms of chlorenchyma. Speaking with reference to a single chamber we may describe these two forms as follows. (1) There is a tightly packed mass of cylindrical cells with their longitudinal axes approximately perpendicular to the leaf surface, and with small intercellular spaces. (*p*, Fig. 1.) This mass lies against the side walls of the chamber, and abuts upon the margin of the roof; here, in the roof, are no stomata. Deep in the leaf, near the middle, the form of the cells changes to that of irregular "collecting" cells (*c*, Fig. 1) which lie against each other, and large parenchymatous elements which receive the products of photosynthesis. (2) A very loose spongy chlorenchyma with large intercellular spaces extends across the floor of the chamber, and separates the two air spaces (*a*, *a'*, Fig. 1) on opposite sides of the leaf. From this loose chlorenchyma extending to either face of the leaf are columns composed of a single series of cells—filaments in effect—which abut upon the epidermal cells and are attached to them. Altogether the chlorenchyma presents a most curious and unique arrangement, in which the palisade may be regarded as really present but, for some secondary reason pushed, so to speak, to the sides of the air chambers. What ecological explanation may be offered? We would suggest that we are dealing here with a very delicate mechanism for controlling the loss of water. It has been remarked that the epidermis is cuticularized on both sides, while the chlorenchyma is free from cuticle. On the assumption that a reduction in turgidity would affect first the chlorenchyma, the rigidity of the columns would thereby be lessened and the epidermal roof would sink in. Such a movement would effect the simultaneous closure of the outer entrances of all the stomata without causing any change in the relative position of the inner guard ridge, within which, the stomata being lifted up somewhat would be the center of oscillation of the guard cells. A very slight movement would suffice for a relatively great change in the total cross section of the outer entrances of the stomata. The writer has sought to determine if a sinking in of the roof actually occurs.

By applying glycerine to thick sections of alcoholic material he has in the majority of cases been able to produce the movement. The results, however, are not convincing, and more exact studies should be carried out upon living material. If this explanation holds good, the position of the palisade cells may be accounted for as contributive to the formation of the diaphragm.

An alternative explanation may be found in the light relations. Vertically placed leaves or their physiological equivalents are commonly supplied with palisade tissue on both faces (isolateral), but hitherto no such peculiar grouping of the chlorenchyma in an isolateral leaf has come to light. Such grouping therefore appears to be secondary and to be accounted for in some other way. The best we can do, therefore, is to admit our ignorance and await experimental evidence.

No further matters in the anatomy of this plant need receive mention at this time beyond the remark that the shrubby character of the plant and its peculiar leaf anatomy clearly separate it from the genus *Solidago*, in which, so far as at present known, no approach to our plant in either regard is to be found, even in halophytic species.

In summarizing we point out the following matters of general interest:

1. The leaf of *Chrysoma pauciflosculosa* is bifacial, isolateral, and of unique structure.

2. Two kinds of hairs are present, which agree with the morphological types found in the Compositae, as defined by Vesque.

3. The stomata correspond closely in structure to those of the majority of halophytes, as described by Warming in his Halofyt Studier, but possess a more specialized inner entrance. They are provided with accessory cells (Nebenzellen), which are not, however, very regularly placed.

4. The arrangement of the mesophyll possibly stands in mechanical relation with the stomata.

5. The perennial shrubby character of the plant and its peculiar leaf anatomy separate it definitely from the genus *Solidago*.

I have to thank Mr. J. E. Kirkwood for the sketch forming Fig. 1.

BONN, March, 1901.